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Systematic review of *Nyctimene cephalotes* and *N. albiventer* (Chiroptera: Pteropodidae) in the Maluku and Sulawesi regions, Indonesia

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Abstract – A univariate and multivariate statistical study of the morphology of island populations of *Nyctimene* in the Maluku region, Indonesia, distinguishes *Nyctimene keasti* Kitchener, 1993, from the Tanimbar and Kai Islands, as a species. The form from the Tanimbar islands is described as a new subspecies of *N. keasti*; it is not associated with *N. cephalotes* as previously considered *in litt. Nyctimene cephalotes* is restricted to Sulawesi and the Maluku region. The Sulawesi population of *N. cephalotes* is described as a distinct new subspecies. The Aru population of *N. albiventer* is somewhat differentiated from the Papua New Guinea population of *N. a. papuanus*; its subspecific status is not determined.

Close island populations of *N. c. cephalotes*, *N. k. keasti* and *N. k.* subsp. nov. show considerable morphological differentiation.

INTRODUCTION

Kitchener *et al.* (1993) examined morphological variation among populations of *Nyctimene albiventer* (Gray, 1863) in the Maluku region. They showed that the population on Aru was morphologically similar to the Papua New Guinea *N. a. papuanus* K. Andersen, 1910; while those on the Kai and Banda Neira Islands (*N. a. keasti* Kitchener, 1993) were distinct from both the Aru form and the nominate subspecies on Halmahera and Ternate Islands.

The discovery of *N. a. keasti* confuses somewhat the previous diagnostic distinction between *N. albiventer* and the closely allied *N. cephalotes* (Pallas, 1767). This distinction had been based on the larger size of *N. cephalotes* and the fact that the females had a dorsum that was much paler than the males, whereas in *N. albiventer* there was no such colour distinction between the sexes (Anderson 1912). A number of *Nyctimene a. keasti* specimens had forearm lengths overlapping those of both *N. a. albiventer* and *N. cephalotes*. Further, female *N. a. keasti* were much paler dorsally than the males.

In the study region, *N. cephalotes* is reported from the following islands: Ambon (fixed as the type locality by Andersen 1912); Seram; Buru, Larat Island (Tanimbar group); Timor and Sulawesi (Andersen 1912; Hill in Corbet and Hill 1992). The records from Larat Island and Timor Island appear to devolve on single specimens collected late last century (Andersen 1912, Goodwin 1979).

Between 1987 and 1993 expeditions by staff from the Western Australian Museum and Museum Zoologicum Bogoriense carried out a survey of the terrestrial vertebrate fauna of South Sulawesi, Maluku and Nusa Tenggara, Indonesia. On these expeditions, series of *Nyctimene* that would be attributed to *N. cephalotes* by earlier authors, were collected from the following islands: Seram; Ambon; Buru; Yamdena and Selaru, Tanimbar group; and South Sulawesi. This paper reports on an examination of these extensive modern collections which allow both a re-appraisal of morphological variation among island populations of *N. cephalotes* and *N. albiventer* and a reassessment of their taxonomy in the study region.

MATERIALS AND METHODS

A total of 142 adult specimens (listed in specimens examined section) was examined. These were from Banda Neira Neira I. (2); Dullah I., Kai Kecil (7); Kai Besar I. (5); Wokam I., Aru islands (27); the Halmahera greup (6); Papua New Guinea (13); Ambon (10); Seram (16); Buru (2); Sulawesi (9); Selaru (13) and Yamdena (32). The localities of these specimens are shown in Figure 1. Apart from the Halmahera group specimens (Australian Museum, Sydney), all specimens are currently lodged in the Western Australian Museum.

Seventeen measurements of skull, dentary and dental characters and six of external body characters (all in mm) were recorded from adult specimens.

The measurements recorded were (all measurement involving teeth were to alveoli): GSL,

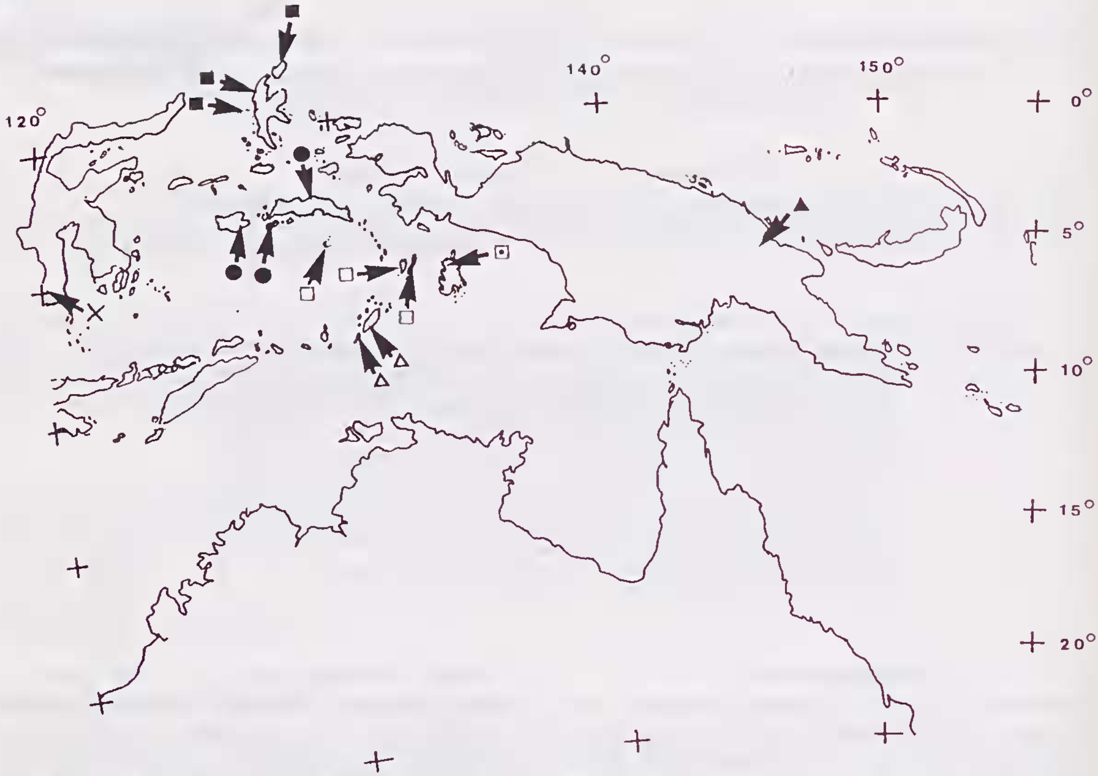


Figure 1 Locality of *Nyctimene* in this study; *N. albiventer albiventer*, ■; *N. a.* subsp. indet., ⊡; *N. a. papuanus*, ▲; *N. keasti keasti*, □; *N. k. tozeri* subsp. nov., Δ; *N. cephalotes cephalotes*, ●; *N. c. aplini* subsp. nov., X.

greatest skull length; CBL, condylobasal length; PIF, minimum length from posterior margin of incisive foramen to palate posterior margin; RL, rostrum length, from anteriomost internal margin of orbit to nares; RH, rostrum height, from upper canine alveoli to level of dorsal surface of nasals; BB, braincase breadth above zygoma; ZW, zygomatic width; M^1M^1 and C^1C^1, width across M^1M^1 and C^1C^1 respectively, from the labial side; C^1M^1 and C_1M_2 upper and lower canine to last molar length; IOB, minimum interorbital breadth; POB, minimum postorbital breadth; MFB, mesopterygoid fossa breadth, at the widest point of the palatal flange; P^4P^4, palatal width between the lingual aspect of P^4P^4; ML, mandible length, from condyle to anteriomost point of dentary; CH, dentary coronoid height; TV, tail to anus length; EAR, basal notch to apex length; FA, forearm length; and MC3–5, metacarpal 3,4 and 5 length.

The skull, dentary and dental characters were measured to an accuracy of 0.01 mm, while the external body characters were measured to 0.1 mm. Terminology used in the description of skull, dentary, dental and external body characters follows Hill and Smith (1984). Pelage descriptions follow the colour terminology of Smithe (1975).

Adults were diagnosed as those specimens with the following sutures fused: basioccipital – basisphenoid, basisphenoid – presphenoid and palatine – maxillary (these sutures are illustrated in Heaney and Peterson 1984: Figure 4).

The effect of sex and island on all characters was examined by multiple regressions for the islands: Yamdena, Selaru, Kai Kecil, Kai Besar, Aru, Ambon, Seram, Sulawesi and Papua New Guinea. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Stepwise canonical variate (discriminant function) analyses (DFA) were run for skull, dentary and dental characters and external characters using all 23 characters for males and females combined, after first testing for sexual dimorphism. A reduced set of five of these characters was used in all presented DFA because in all instances they provided similar DF plots to the full set of 23 characters. This reduced set of characters was selected in all these analyses because the sample size of the smallest *a priori* group selected was always less than the total number of characters. This reduced set of characters was selected because they provided values that minimise Wilk's Lambda.

STATISTICS: RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size for each island are presented in Table 1, this paper, and Kitchener *et al.* (1993: Table 1) for all characters examined.

Multiple regressions

Multiple regressions were run for skull, dentary, dental and external characters on sex and nine island populations. The islands of Buru, Banda Neira, Halmahera, Ternate and Moratai were excluded because of their small sample size and/ or absence of either males or females (Table 2).

Sex

Metacarpal 3–5 lengths and postorbital breadth were significantly influenced by sex ($F_{1,96}$ = 6.11, P = 0.015; $F_{1,96}$ = 4.67, P = 0.033; $F_{1,96}$ = 4.653, P = 0.033; and $F_{1,96}$ = 4.639, P = 0.034, respectively.

Island

Only postorbital breadth was not highly (<.01) significantly related to island. Clearly there was considerable difference in morphology between these island populations.

Interactions

There were no significant interactions.

Multivariate analyses

Because the multiple regression analysis involved testing a large number of interactions, some of these tests will be significant at 0.05>P>0.01 by chance alone. For this reason, none of the characters measured were considered to be markedly influenced by sex. As a result both males and females are combined for all 23 characters examined in the following DFA.

All populations

The DFA was first run using all 23 skull, dental, dentary and external body characters and the islands Aru, Kai Besar, Kai Kecil, the Halmahera group (Halmahera, Ternate and Morotai) Papua New Guinea, Selaru and Yamdena (Tanimbar Islands), Seram, Ambon and Sulawesi. Banda Neira and Buru were ungrouped because there were only two individuals from each of these islands. The above analysis was then repeated using only five characters (forearm length, FA; ear length EAR; C_1M_2 length, C_1M_2; width across M^1M^1 from labial side, M^1M^1; and rostral length, RL). This analysis extracted four significant functions which together explained 99.6% of the variation, with 68.0% of individuals classified to their correct island group.

From Figure 2, three broad groups were defined:

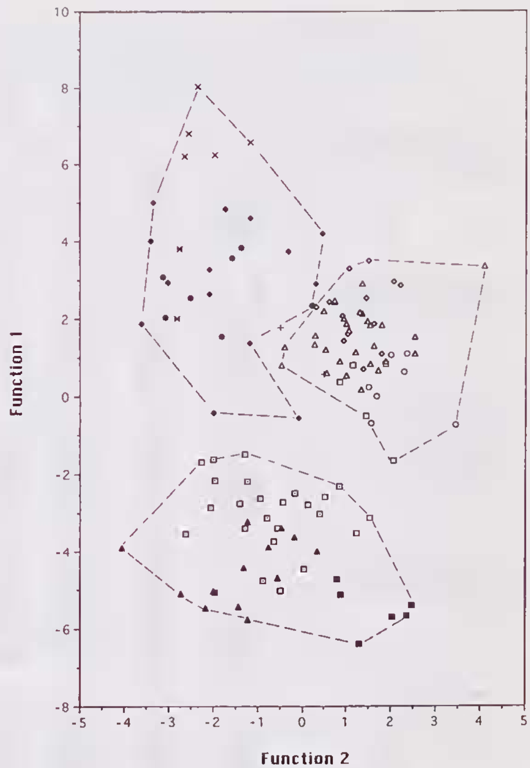


Figure 2 Canonical variate analysis on the following island populations: Aru, ⊡ ; Kai Besar, □; Kai Kecil, ○; the Halmahera group (Halmahera, Ternate and Morotai), ■; Papua New Guinea, ▲; Selaru ◊; and Yamdena, Δ (Tanimbar group); Seram, ♦; Ambon, ●; and Sulawesi, X; Banda Beira +, and Buru ✱, were ungrouped. The DFA plots of functions 1 and 2 were based on a selection of five characters (skull, dentary, and external body), with males and females combined.

the Ambon group (Ambon-Seram-Buru-Sulawesi); the Kai group (Kai and Tanimbar islands); and the Halmahera group (Halmahera, Aru and Papua New Guinea). When a DFA was again run using the reduced set of five characters and these three island groups, the analysis extracted two significant functions (Figure 3). Function 1, which explained 78.9% of the variance, separated the Ambon and Kai groups from the Halmahera group. The character loading heavily on the standardised canonical variate coefficients (>0.6) on this function was C_1M_2 length (Table 3). Function 2, which separated the Ambon group from the Kai group, explained 21.1% of the variation. The characters loading heaviest (>0.6) on Function 2 were forearm and ear length (Table 3). A total of 99.2% of individuals was correctly classified to their appropriate island group. One specimen of the Ambon group classified to the Kai

Table 1 Measurements, in mm, for skull, dentary, dental and external body characters (see Material and Methods section for explanation of character codes) of adult *Nyctimene cephalotes aplini*, *N. c. cephalotes*, *N. keasti keasti* and *N. k. tozeri*. N, sample size; $\bar{X}$, mean; SD, standard deviation; MIN, minimum; MAX, maximum.

		GSL	CBL	PIF	RL	RH	BB	ZW	M^1M^1	C^1C^1
Nyctimene cephalotes aplini	N	9	9	9	9	9	9	9	9	9
(Sulawesi)	$\bar{X}$	31.74	30.22	12.77	6.39	7.25	13.40	21.37	9.56	5.80
	SD	0.47	0.33	1.48	0.39	0.27	0.27	0.48	0.19	0.27
	MIN	31.05	29.71	11.76	5.72	6.64	12.95	20.74	9.31	5.43
	MAX	32.42	30.67	13.54	7.00	7.59	13.81	22.24	9.92	6.17
N. cephalotes cephalotes	N	25	25	26	26	26	26	26	26	26
(Seram, Ambon, Buru)	$\bar{X}$	30.13	28.66	12.23	5.94	7.05	12.76	19.80	8.88	5.57
	SD	0.68	0.64	0.48	0.27	0.34	0.37	0.72	0.32	0.24
	MIN	28.32	26.98	11.45	5.27	6.16	11.59	17.81	7.81	5.04
	MAX	31.05	29.69	13.70	6.39	7.79	13.39	20.90	9.42	6.02
N. cephalotes	N	34	34	35	35	35	35	35	35	35
(Sulawesi, Seram,	$\bar{X}$	30.56	29.07	12.37	6.06	7.10	12.93	20.21	9.06	5.63
Ambon, Buru)	SD	0.95	0.90	0.53	0.36	0.33	0.44	0.96	0.42	0.26
	MIN	28.32	26.98	11.45	5.27	6.16	11.59	17.81	7.81	5.04
	MAX	32.42	30.67	13.70	7.00	7.79	13.81	22.24	9.92	6.17
N. keasti keasti	N	12	12	12	12	12	12	12	12	12
(Kai Besar, Kai Kecil)	$\bar{X}$	28.77	27.28	12.06	5.52	6.36	12.34	19.06	8.16	5.46
	SD	0.50	0.52	0.26	0.34	0.37	0.31	0.33	0.24	0.24
	MIN	28.04	26.02	11.58	4.96	5.75	11.64	18.63	7.66	5.18
	MAX	29.38	27.88	12.47	6.00	6.96	12.68	19.71	8.45	5.80
N. keasti tozeri	N	44	44	44	44	44	44	44	44	44
(Selaru, Yamdena)	$\bar{X}$	29.50	27.74	11.85	5.73	6.72	12.72	19.34	8.70	5.57
	SD	0.56	0.48	0.43	0.27	0.28	0.28	0.45	0.23	0.18
	MIN	28.45	26.64	10.92	5.07	6.22	12.20	18.11	8.09	5.24
	MAX	30.78	28.74	12.81	6.30	7.30	13.94	20.40	9.09	5.96
N. keasti	N	56	56	56	56	56	56	56	56	56
(Kai Is, Tanimbar Is)	$\bar{X}$	29.35	27.65	11.91	5.68	6.64	12.64	19.28	8.58	5.55
	SD	0.62	0.52	0.41	0.30	0.33	0.33	0.44	0.32	0.20
	MIN	28.04	26.02	10.92	4.96	5.75	11.64	18.11	7.66	5.18
	MAX	30.78	28.74	12.81	6.30	7.30	13.94	20.40	9.09	5.96

group. Of the two "ungrouped" Banda Neira specimens, both classified to the Kai group.

These three island groups represent three described taxa as will be discussed below. These taxa are *Nyctimene cephalotes* (Ambon, Seram, Buru, Sulawesi); *N. keasti* (Kai and Tanimbar groups, with Banda Neira specimens referred to this group); and *N. albiventer* (Halmahera, Aru and Papua New Guinea).

Nyctimene cephalotes populations

A DFA was run for all 23 characters for the islands Ambon, Seram and Sulawesi, with Buru unallocated. A reduced set of five characters was selected from this above analysis. These were: condylobasal length, CBL; zygomatic width, ZW; mesopterygoid fossa breadth, MFB; mandible length, ML; and upper canine to first molar cusp length, C^1M^1. The selection of only skull and mandible characters in this subset of five characters enabled the inclusion of an additional sample of Sulawesi individuals (which were missing some external measurements) to be included in this DFA. This latter DFA extracted two significant functions which explained 100% of the variation (Figure 4). A total of 73.5% of individuals was correctly classified to their correct island population, with misclassification occurring between the Ambon and Seram populations. One of the Buru specimens was allocated by DFA to the Seram population and the other to the Ambon population.

The DFA was run again using 23 characters for the two *a priori* groups: Sulawesi and the group Ambon, Seram and Buru. A subset of five characters (condylobasal length; C^1M^1 length; M^1M^1 breadth; rostrum height; incisive foramen to posterior palatal length) was selected from the above analysis. This latter analysis extracted a very significant function and all individuals were correctly classified to their appropriate group (Figure 5). The characters loading most heavily on this function were CBL (1.9), C^1M^1 (–1.4) and M^1M^1 (0.6) (Table 4).

The type locality of the nominate subspecies of

Table 1 (continued)

C^1M^1	IOB	POB	MFB	P^4P^4	ML	CH	C_1M_2	FA	MC3	MC4	MC5	TV	EAR
9	9	9	9	9	9	9	9	5	5	5	5	5	5
10.62	6.44	6.18	5.18	6.02	23.79	13.92	11.96	68.6	49.1	44.8	48.6	25.1	16.2
0.28	0.40	0.60	0.13	0.23	0.41	0.31	0.25	0.6	1.9	2.2	2.7	1.0	0.3
10.34	6.03	5.51	4.96	5.47	23.20	13.41	11.66	68.1	47.4	42.3	45.2	23.7	15.8
11.11	7.17	7.39	5.37	6.26	24.37	14.47	12.41	69.5	51.8	47.7	52.0	26.2	16.5
26	26	26	25	26	26	26	26	24	24	24	24	24	24
10.16	5.65	5.77	5.16	5.58	22.55	12.99	11.46	63.4	45.1	41.8	44.6	22.4	14.2
0.43	0.35	0.44	0.20	0.23	0.67	0.72	0.44	2.1	1.6	1.5	1.7	1.3	0.6
9.02	4.94	5.17	4.79	4.89	21.02	11.47	10.21	59.1	41.4	38.6	40.2	20.6	12.9
10.82	6.13	6.94	5.61	5.94	23.69	14.23	12.09	67.6	48.0	44.1	47.2	24.8	15.2
35	35	35	34	35	35	35	35	29	29	29	29	29	29
10.28	5.85	5.88	5.16	5.69	22.87	13.23	11.59	64.3	45.8	42.3	45.3	22.9	14.5
0.44	0.50	0.51	0.19	0.30	0.82	0.76	0.46	2.7	2.2	2.0	2.4	1.6	1.0
9.02	4.94	5.17	4.79	4.89	21.02	11.47	10.21	59.1	41.4	38.6	40.2	20.6	12.9
11.11	7.17	7.39	5.61	6.26	24.37	14.47	12.41	69.5	51.8	47.7	52.0	26.2	16.5
12	12	12	12	12	12	12	12	12	12	12	12	12	12
9.57	5.69	6.02	4.76	5.19	21.49	12.86	10.84	58.2	42.2	38.5	40.6	20.7	15.0
0.24	0.24	0.35	0.17	0.10	0.51	0.31	0.26	1.3	1.1	0.7	1.0	1.5	0.5
8.98.	5.29	5.21	4.50	5.03	20.58	12.33	10.27	55.1	40.7	37.5	38.7	18.6	14.2
9.80	6.12	6.44	5.05	5.38	22.11	13.32	11.18	59.7	44.5	39.6	42.7	24.1	15.6
44	44	44	44	44	44	44	44	44	44	44	44	44	44
10.01	5.81	5.66	5.00	5.60	22.00	13.38	11.28	60.1	43.5	39.6	42.1	21.3	15.4
0.33	0.28	0.41	0.17	0.19	0.49	0.47	0.29	1.2	1.0	1.1	1.0	1.6	0.6
8.39	5.30	5.03	4.56	5.24	21.04	12.34	10.76	58.0	41.6	37.5	40.0	18.0	14.3
10.50	6.49	6.65	5.39	5.97	23.10	14.46	12.10	63.0	45.7	43.1	44.2	25.4	16.9
56	56	56	56	56	56	54	56	56	56	56	56	56	56
9.91	5.78	5.74	4.95	5.51	21.89	13.26	11.18	59.7	43.2	39.4	41.8	21.2	15.3
0.36	0.27	0.42	0.20	0.24	0.53	0.49	0.34	1.4	1.2	1.1	1.2	1.6	0.6
8.39	5.29	5.03	4.50	5.03	20.58	12.33	10.27	55.1	40.7	37.5	38.7	18.0	14.2
10.50	6.49	6.65	5.39	5.97	23.10	14.46	12.10	63.0	45.7	43.1	44.2	25.4	16.9

N. cephalotes was fixed as Ambon by Andersen (1912). The above documentation of the morphological separation of the Sulawesi population from *N. c. cephalotes* warrants its description as a new subspecies of *N. cephalotes*.

Nyctimene keasti populations

DFA was run for all 23 characters for the islands Kai Besar, Kai Kecil, Selaru and Yamdena, with Banda Neira unallocated. A reduced set of five characters was selected from this above analysis. These were palatal width between the lingual aspect of P^4P^4; ear length; forearm length; braincase breadth; minimum length from posterior margin of incisive foramen to palate posterior margin. This latter DFA produced two significant functions, which combined explained 98.4% of the variation (Figure 6). A total of 81.5% of individuals were correctly classified to their appropriate island, with misclassification occurring between the two Tanimbar islands. One of the unallocated Banda Neira specimens classified with the Selaru population and the other with the Yamdena population.

The DFA run with 23 characters and only two *a priori* groups: Tanimbar group (Selaru and Yamdena) and Kai group (Kai Kecil and Kai Besar) produced a similar discriminant histogram to that produced from a subset of the five characters that were selected from the above analysis (palate breadth at P^4P^4; incisive foramen to posterior palate length, PIF; braincase breadth, BB; postorbital breadth, POB; and forearm length, FA). The function extracted from this latter analysis was highly significant and resulted in all individuals being correctly allocated to their appropriate group (Figure 7). The characters loading heavily (>0.6) on this function were P^4P^4, FA and BB (Table 5).

The type locality of the nominate subspecies of *N. keasti* is Pulau Dullah, Kai Kecil. The above analysis documents clearly the morphological separation of the Tanimbar form from *N. k. keasti*. It indicates that the Tanimbar form warrants description as a new taxon. It also shows that some

Table 2 Multiple regressions on sex and island populations of *Nyctimene albiventer*, *N. cephalotes* and *N. keasti* for skull, dentary, dental and external body characters. F values are presented for the main effects and their interactions. For explanation of character codes see Material and Methods section. Significance levels are *, 0.05>p>0.01; ** 0.01>p>0.001; ***, p<0.001.

CHARACTER	MAIN EFFECT SEX	MAIN EFFECT ISLAND	INTERACTION SEX. ISLAND
GSL	0.354	54.340***	0.774
CBL	0.050	45.776***	0.968
PIF	0.646	27.866***	0.831
RL	0.530	41.475***	0.911
RH	0.015	10.427***	0.795
BB	0.335	17.716***	0.817
ZW	0.618	26.450***	0.877
M^1M^1	0.367	17.584***	0.774
C^1C^1	1.770	5.361***	1.378
C^1M^1	0.083	32.995***	0.430
IOB	0.110	15.210***	1.012
POB	4.631*	0.959	0.875
MFB	0.000	16.366***	0.376
P^4P^4	2.096	6.823***	0.367
ML	0.063	41.255***	0.425
CH	0.010	28.720***	1.173
C_1M_2	0.084	45.256***	0.695
FA	1.887	62.079***	0.725
MC3	6.110*	42.895***	0.914
MC4	4.667*	46.285***	1.117
MC5	4.653*	41.120***	1.070
TV	2.469	3.331**	0.818
EAR	0.422	30.529***	0.571
d.f.	1,96	8,96	8,96

morphological differentation has occurred between the two Kai Island populations.

Nyctimene albiventer populations

Kitchener *et al.* (1993) examined the morphological differences between the Halmahera group (*N. a. albiventer*), Aru and Papua New Guinea populations (attributed to *N. a. papuanus*) and Kai group (*N. a. keasti*) populations. The removal of the form *keasti* from association with *N. albiventer* in this study may affect the perceived morphological association between these remaining populations of *N. albiventer* using DFA.

DFA was run on all 23 characters for the islands: Halmahera, Aru and PNG. A reduced set of five characters was selected from the above analysis. Those were palatal breadth at P^4P^4, P^4P^4; rostrum height, RH; C^1M^1 length; mesopterygoid fossa breadth, MFB; and greatest skull length, GSL. The DFA plots based on these five characters produced two significant functions (Figure 8). A total of 90.5% of individuals was correctly classified to their appropriate island. Three individuals from Aru were misclassified to PNG, and one individual from PNG was misclassified to Aru. Function 1, which explains 74.5% of the variation, separates the Halmahera group from both the Aru Island and PNG populations. The characters loading heavily (>6) on Function 1 were P^4P^4 and GSL (Table 6). Function 2, which explains 25.5% of the variation, separates the Halmahera group from the PNG population. The characters loading heavily (>0.6) on Function 2 were C^1M^1 and RH (Table 6).

When the DFA was run for the Aru and PNG populations and for a subset of five characters (ear

Table 3 Canonical variate function coefficients from DFA between the *Nyctimene* species (*N. albiventer*, *N. cephalotes* and *N. keasti*). Standardised values, followed by (in brackets) unstandardised values, for skull, dental and external body characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1	FUNCTION 2
C_1M_2	0.6941 (1.7737)	0.5583 (1.4266)
FA	0.4366 (0.2167)	–0.8945 (–0.4438)
EAR	–0.0297 (–0.0373)	0.9784 (1.2309)
RL	0.4542 (1.5569)	–0.0234 (–0.0802)
M^1M^1	–0.4455 (–1.1545)	–0.4087 (–1.0591)
Constant	–30.0241	2.4944
Explained variation (%)	78.9	21.1

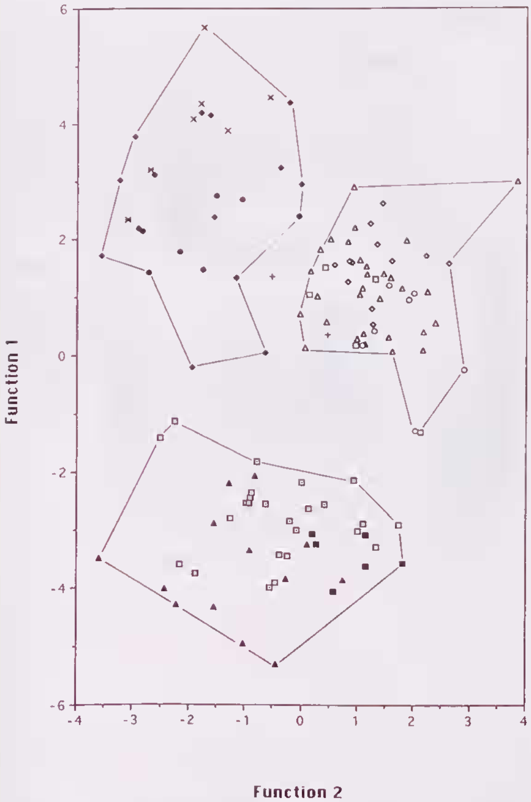


Figure 3 Canonical variate analysis on three groupings of islands, (i), Aru, Halmahera and Papua New Guinea; (ii) Kai Besar, Kai Kecil, Yamdena, and Selaru; and (iii) Seram, Ambon, Buru and Sulawesi: Banda Neira was ungrouped. The DFA plots of functions 1 and 2 were based on a selection of the same five characters as in Figure 2, with males and females combined. Symbols are as for Figure 2.

Table 4 Canonical variate function coefficients from DFA between the population of *Nyctimene cephalotes aplini* from Sulawesi and the combined populations of *N. c. cephalotes* from Seram, Ambon and Buru. Standardised values, followed by (in brackets) unstandardised values, for skull and dental characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1
CBL	1.9328 (3.3396)
C^1M^1	–1.3704 (–3.4858)
M^1M^1	0.6323 (2.1542)
RH	–0.4987 (–1.5196)
PIF	–0.4524 (–0.9386)
Constant	–58.3252

length, EAR; rostrum height, RH; rostrum length, RL; C^1M^1 length and interorbital breadth, IOB), the function extracted was highly significant with 94.9% of individuals correctly classified to their appropriate population (Figure 9). Only two Aru individuals were misclassified to the PNG group. The characters loading heaviest (>0.6) on this function were C^1M^1 and RH (Table 7).

Summary of multivariate analyses

The above DFA supports the view that the recently described taxon *keasti* is equally distinct from both *N. albiventer* and *N. cephalotes* and should be treated as a species. Further, it shows that the Tanimbar populations, rather than being referred to *N. cephalotes* as indicated by Andersen (1912) and Hill in Corbet and Hill (1992), are more closely allied to *N. keasti*.

The Sulawesi populations referred to *N. cephalotes* are distinct from Maluku population of the species and are identified as a subspecies of *N. cephalotes*.

The species *N. cephalotes*, *N. keasti* and *N. albiventer* are rediagnosed for the study region and the Sulawesi and Tanimbar forms described as new

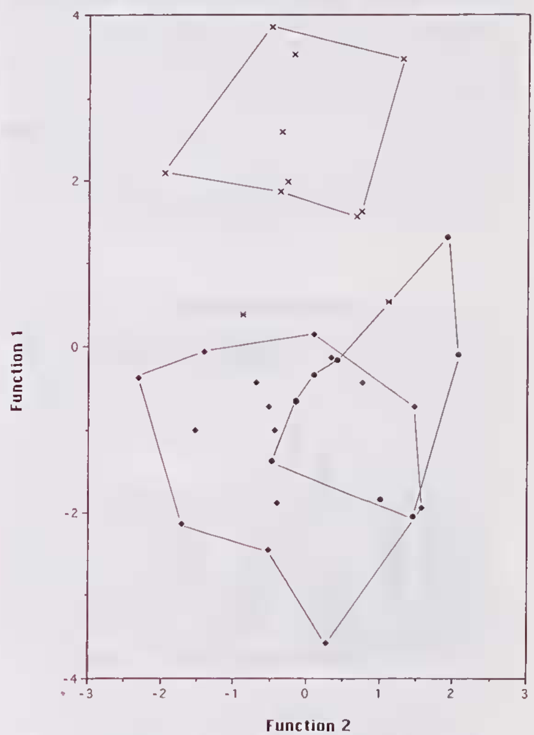


Figure 4 Canonical variate analysis among three island populations of *Nyctimene cephalotes* (Seram, Ambon and Sulawesi) with the Buru population ungrouped. The DFA plots of functions 1 and 2 were based on a selection of five skull characters with males and females combined. Symbols as for Figure 2.

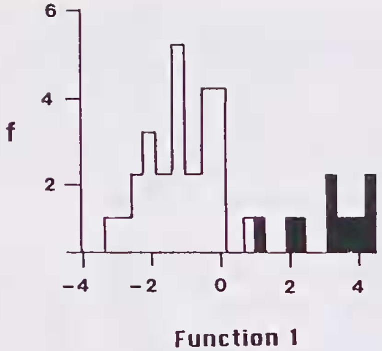


Figure 5 Canonical variate analysis between the Sulawesi population (*Nyctimene cephalotes aplini* subsp. nov.) (■) and those of the group of Seram, Ambon and Buru (*N. c. cephalotes*) (□). The histogram for function 1 was based on a selection of five skull characters, with males and females combined.

subspecies below.

The Aru form, is still phenetically close to the Papua New Guinea form, but is more differentiated morphologically from the Papua New Guinea form than was thought to be the case in Kitchener *et al.* (1993). Its subspecific status is not determined. Within the island groups of Tanimbar and Kai there has been considerable morphological differentiation between populations of subspecies of *N. keasti* inhabiting different islands. This has occurred to a lesser extent also between the Ambon and Seram populations of *N. c. cephalotes*.

SYSTEMATICS

Nyctimene cephalotes (Pallas, 1767)

Diagnosis

Nyctimene cephalotes differs from *Nyctimene*

Table 5 Canonical variate function coefficients from DFA between populations of *Nyctimene keasti keasti* from the Kai Islands and *N. k. tozeri* from the Tanimbar Islands. Standardised values, followed by (in brackets) unstandardised values, for skull, dental and external body characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1
P^4P^4	0.6922 (3.9545)
FA	–0.7606 (–1.9787)
BB	0.7532 (2.5839)
POB	–0.4283 (–1.0462)
PIF	0.3125 (0.2625)
Constant	–40.5598

Table 6 Canonical variate function coefficients from DFA between populations of *Nyctimene albiventer*, *N. a albiventer*, *N. a. papuanus* and *N. a.* subsp. indet. from Halmahera group, and Papua New Guinea and Aru, respectively. Standardised values, followed by (in brackets) unstandardised values, for skull and dental characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1	FUNCTION 2
P^4P^4	0.7335 (3.0491)	0.4262 (1.7717)
C^1M^1	0.1907 (0.7626)	–0.9287 (–3.7137)
RH	–0.2628 (–0.8189)	0.8977 (–2.7979)
MFW	–0.5806 (–2.3344)	0.1779 (0.7151)
GSL	0.6701 (1.0692)	0.1438 (0.2295)
Constant	–35.8486	–3.3963
Variation explained (%)	74.5	25.5

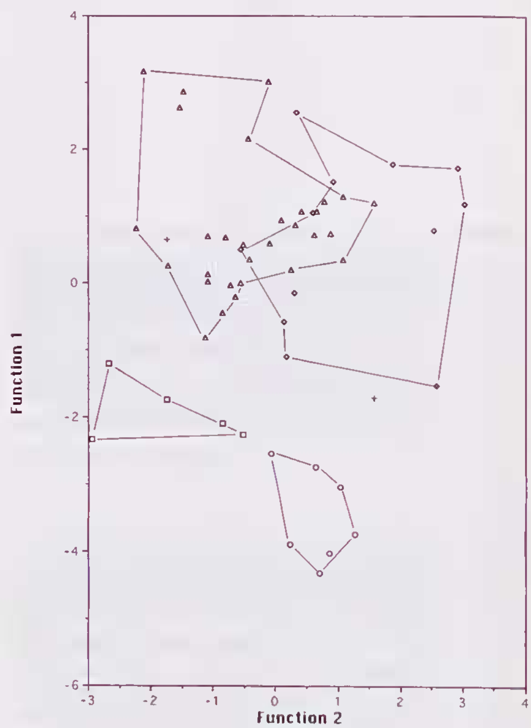


Figure 6 Canonical variate analysis among four island populations of *Nyctimene keasti*: Kai Besar, Kai Kecil (*N. k. keasti*), Selaru and Yamdena (*N. k. tozeri* subsp. nov.). The Banda Neira population was ungrouped. The DFA plots of functions 1 and 2 were based on a selection of five skull, dentary and external body characters, with males and females combined. Symbols as for Figure 2.

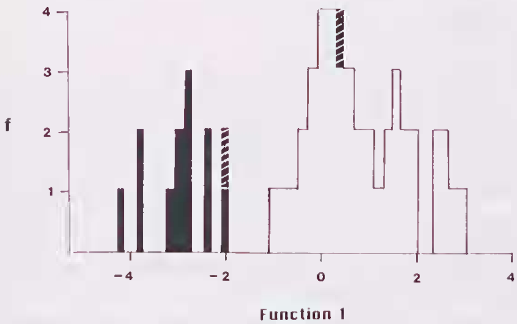


Figure 7 Canonical variate analysis between *Nyctimene keasti* populations from the Kai Island group (Kai Besar and Kai Kecil) (*N. k. keasti*) (■) and the Tanimbar Island group (Selaru and Yamdena) (*N. k. tozeri* subsp. nov.) (□). The Banda Neira population was ungrouped (⊠). The histogram for Function 1 was based on a selection of five characters (skull, dentary and external body), with males and females combined.

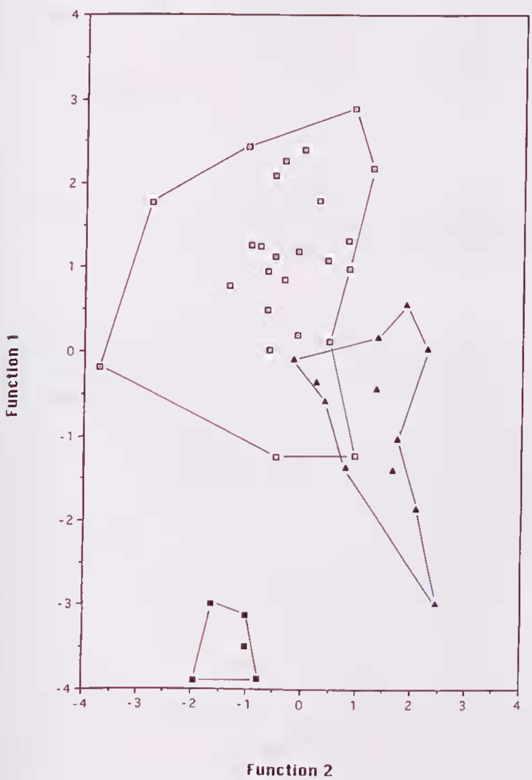


Figure 8 Canonical variate analysis between *Nyctimene albiventer* populations from the Halmahera island group (Halmahera, Morotai and Ternate) (*N. a. albiventer*), Aru (*N. a.* subsp. indet.) and Papua New Guinea (*N. a. papuanus*). The DFA plots of functions 1 and 2 were based on a selection of 5 characters (skull and dental), with males and females combined. Symbols as for Figure 2.

Table 7 Canonical variate function coefficients from DFA between populations of *Nyctimene albiventer* from Aru islands and Papua New Guinea. Standardised values, followed by (in brackets) unstandardised values for skull, dental and external body characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1
C^1M^1	0.7909 (3.0302)
RH	–0.6888 (–2.1155)
EAR	0.5633 (0.6949)
RL	0.4382 (1.6215)
IOB	–0.4345 (–1.4417)
Constant	–23.1370

albiventer by averaging larger in all measurements (Table 1). Incisive foramen to posterior palatal length shorter relative to postorbital breadth (Figure 10); C_1M_2 length generally longer relative to M^1M^1 length (Figure 11); and forearm longer relative to ear length (Figure 12). Female dorsum paler than that of males.

It differs from *Nyctimene keasti* by averaging larger in all measurements except for cranial height (Table 1). Condylobasal length generally longer relative to both rostrum height, interorbital breadth and cranial height (Figure 13A,B,C, respectively); and forearm longer relative to ear length (Figure 12).

Nyctimene cephalotes aplini Kitchener, subsp. nov.

Holotype

Museum Zoologicum Bogoriense Number MZB 15903; adult male; weight 46 g; carcase fixed in 10% formalin and preserved in 75% ethanol; skull and mandibles separate; collected by Drs Augustine Suyanto on 28 July 1990.

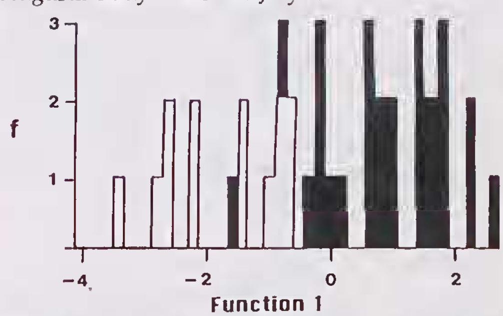


Figure 9 Canonical variate analysis between two populations of *Nyctimene albiventer*: Aru (*N. a. aruensis* subsp. nov.) (■) and Papua New Guinea (*N. a. papuanus*) (□). The histogram for function 1 was based on a selection of five characters (skull, dental and external body), with males and females combined.

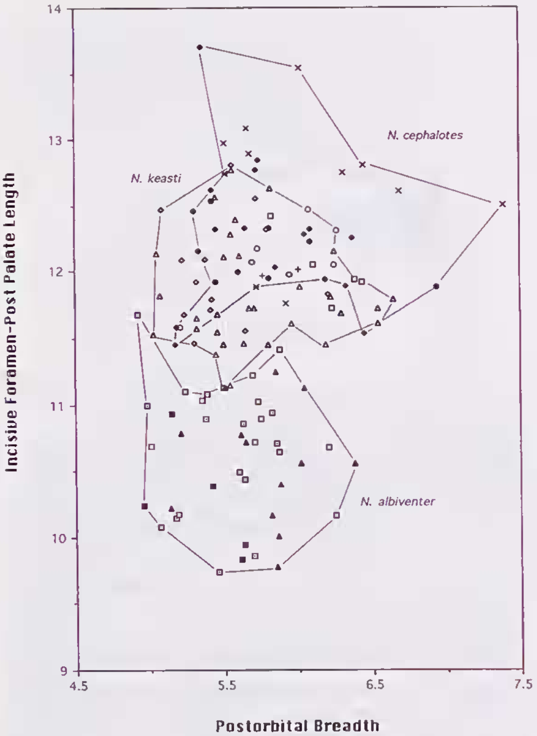


Figure 10 Plot of incisive foramen to posterior palate length *versus* postorbital breadth for all island populations of *Nyctimene* studied. Males and females combined. Symbols as for Figure 2.

Paratypes

Tomado, Lake Lindu area Central Sulawesi, WAM M27659 A ♀, skin and skull; Soroako, Sulawesi Selatan, WAM M27676 A ♀, skin and skull; WAM M33145, near Bontobonto, Sulawesi Selatan (*c.* 5°07'S, 119°39'E), A ♀, spirit carcase and skull; Maros, Sulawesi Selatan (*c.* 4°59'S, 119°35'E), WAM (M33146, M33207), 2♂♂ skin and skull, WAM (M33208, M33210–12), 4♂♂, spirit carcase and skull.

Type locality

Maros, Sulawesi Selatan (= S. Sulawesi) (*c.* 4°59', 119°35'E), altitude *c.* 50 m; mist-netted.

Diagnosis

Nyctimene cephalotes aplini differs from *N. c. cephalotes* in averaging larger in all skull, mandible and external measurements; in some it is absolutely larger (Table 1). Condylobasal length greater relative to both mesopterygoid fossa breadth, MFB, and C^1M^1 length (Figures 14A,B, respectively); and zygomatic width greater relative to MFB (Figure 15).

Description

Skull, dentary and dentition

Large skull with greatest length 31.7 ± 0.47, broad zygomatic width 21.4 ± 0.48, palate long and broad both anteriorly, with C^1C^1 breadth 5.8 ± 0.27, and posteriorly, with M^1M^1 breadth 9.6 ± 0.19; rostrum short, nasal dorsal surface almost horizontal, occasionally with dorsal distal inclination; rostrum high; premaxillary part of nares terminates directly above incisors or projects slightly anterior to them; braincase typical of *N. cephalotes* with cranium inflated to maximum height at junction of strong sagittal and weak postorbital crests; postorbital breadth large; usually deeply basined and opens anteriorly into deep frontal sulcus; frontals converging slightly posteriorly; sagittal and lambdoidal crests moderately high; incisive foramen subcircular, reach posteriorly almost to line joining P^2P^2 anterior face; posterior palate extends well beyond M^1, its margin a broad U shape; basi- and presphenoid median ridge prominent; pterygoid process low and slightly curved ventrally and laterally.

Upper tooth row slightly curved; upper incisors in contact, sited close to line joining C^1C^1

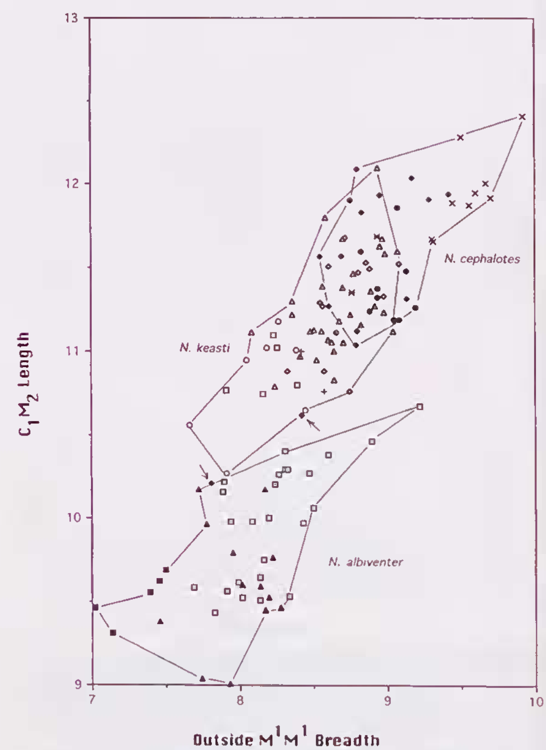


Figure 11 Plot of C_1M_2 length *versus* outside M^1M^1 breadth for all island population of *Nyctimene* studied. Males and females combined. Symbols as for Figure 2.

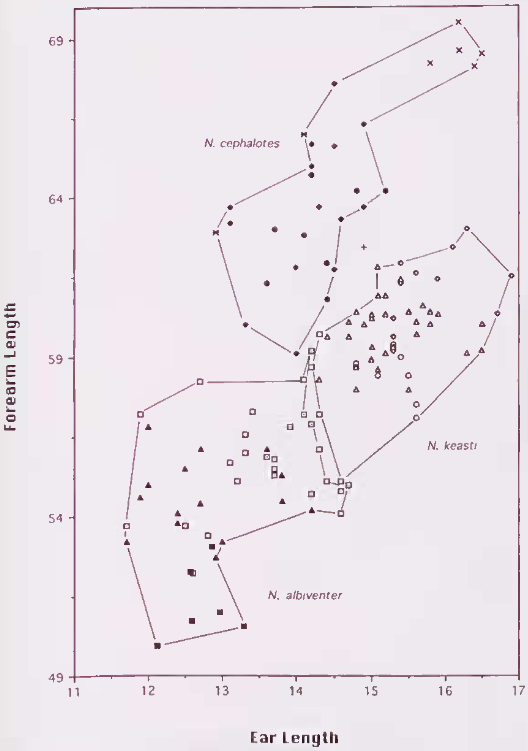


Figure 12 Plot of forearm length *versus* ear length for all island populations of *Nyctimene* studied. Males and females combined. Symbols as for Figure 2.

anteriormost face, not in contact with C^1; C^1 prominent cusp with gentle lingual ridge connecting to lingual and posterior cingulum, lingual cingulum occasionally with posterolingual cusplet; C^1 with moderate secondary labial cusp on posterolabial ridge, this cusp not apparent in specimens with worn teeth; P^2 subcircular, buccal area half to three-quarters that of incisors, widely spaced between C^1 and P^3; P^3 occlusal view suboval, with prominent labial cusp and much lower separate lingual cusp; posterior basal shelf well defined and forms slight basin, occlusal area slightly larger than P^4; P^4 occlusal view subrectangular with posterolingual salient from basal shelf; labial cusp lower than that of P^3, lingual cusp less clearly defined than that of P^3, with longer posterior ridge that reaches almost to posterolingual edge of posterior basal shelf, lingual cusp closer in height to labial cusp than in P^3; M^1 subrectangular, labial cusp low and only slightly taller than lingual cusp, posterior basal shelf definition similar to that of P^4; C_1 not in contact with each other or with P_2; P_2 suboval, slightly taller than C_1 cingulum; P_3 with tall labial cusp with gently sloping anterior and posterior flanges approximately in line of toothrow, shorter labial cusp distinct; P_4 considerably shorter than P_3, labial cusp taller than lingual cusp but less so than in P_3, these cusps connected by commissure that arcs around anterior face of tooth; M_1 longer and narrower than P_4 but with both labial and lingual cusps much reduced on those of P_4; M_2 small, about half occlusal area of M_1. M_1 posterior shelf slightly larger than that of P_3 and P_4.

Externals (measurements of ethanol preserved specimens followed by, in square brackets, 'cabinet' skin specimens).

Large body and ears. For example, forearm long 68.6 (68.1–69.5) 5 and [70.9 (69.0–73.0) 4]; ear long 16.2 (15.8–16.5) 5 and [16.6 (15.1–18.3) 4] and tail length 25.1 (23.7–26.2) 5 and [23.3 (19.9–27.2) 4]. Wing membrane from phalanx 1 of digit 2 in all nine specimens examined.

Males and females with similar coloured pelage. Slight colour patterning on dorsum and venter: neck to lower scapular region a broad band of paler Smoke Gray to Buff Yellow, occasionally tinged with Clay Color on shoulders and behind ears; remainder of back a darker Drab with hairs in mid dorsal region *c.* 9 long, merges into Fawn Color to Clay Color on flanks; median central dorsal stripe from head to tail, 2–6.5 wide and Olive Brown. Basal one-third to half of dorsum hairs pale-dark Olive Brown. Forehead and face Drab to Cinnamon; chest and abdomen Straw Yellow to Buff Yellow with abdomen occasionally Smoke Gray merging to darker Grayish Olive at flanks. Uropatagia Fuscous. Spectrum Yellow spots on patagia, ears, and skin covering all digits, particularly noticeable on forearm where spots often merge to form a broad line of colour.

Distribution

Central and South Sulawesi, probably also North Sulawesi.

Etymology

Named after our colleague, Dr Ken Aplin, Western Australian Museum, who participated in the expedition to Timor Island, Nusa Tenggara Timur, and who frequently has assisted us interpret the Indo-Malay mammal fauna.

Nyctimene cephalotes cephalotes (Pallas, 1767)

Vespertilio cephalotes Pallas, 1767: 10, pls 1,2 "Moluccas".

Vespertilio cephalotes melinus Kerr, 1792: 98. Type locality restricted to Amboina by Andersen (1912).

Cephalotes pallasi Geoffroy, 1810: 107 (renaming of *cephalotes* Pallas).

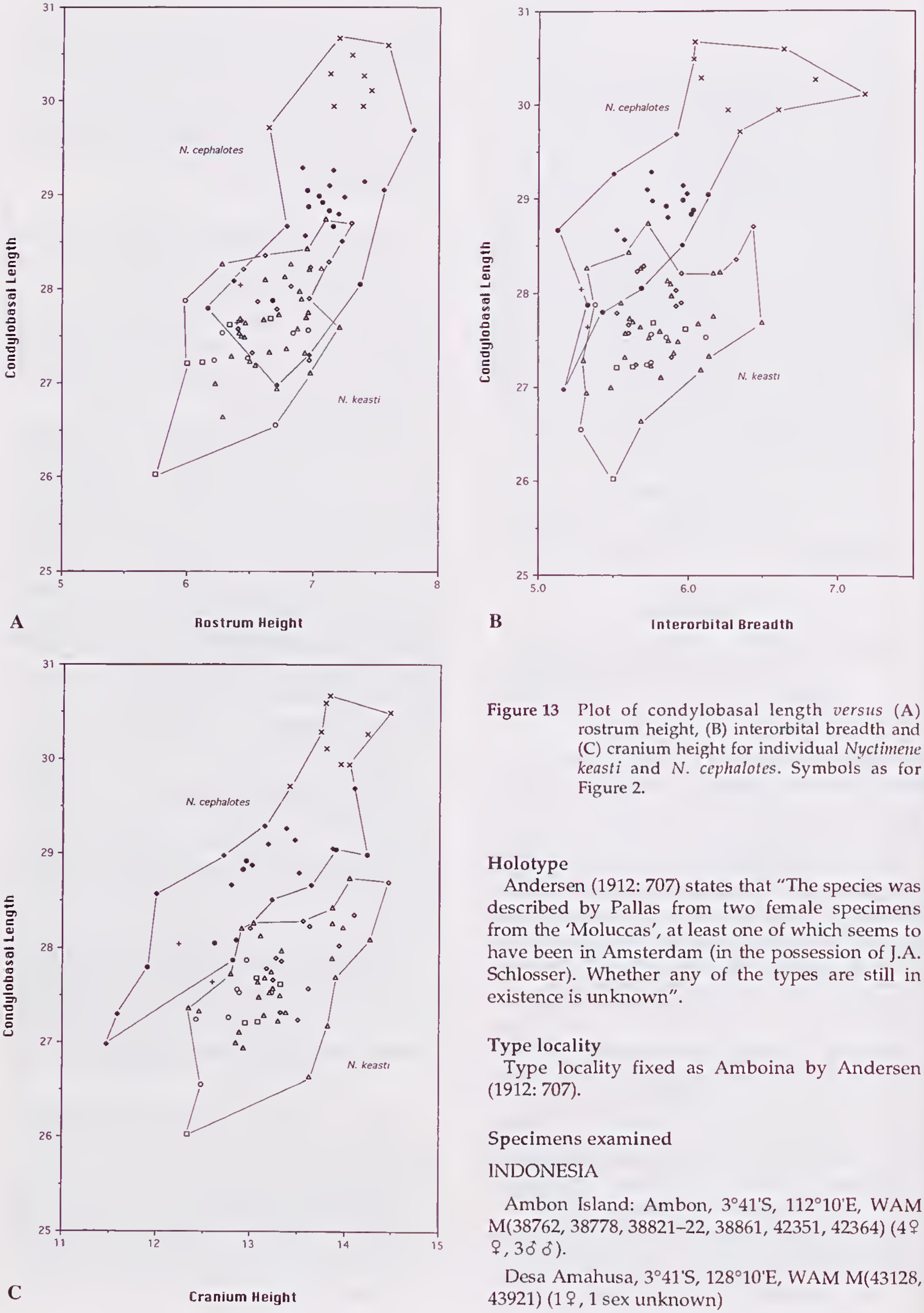


Figure 13 Plot of condylobasal length *versus* (A) rostrum height, (B) interorbital breadth and (C) cranium height for individual *Nyctimene keasti* and *N. cephalotes*. Symbols as for Figure 2.

Holotype

Andersen (1912: 707) states that "The species was described by Pallas from two female specimens from the 'Moluccas', at least one of which seems to have been in Amsterdam (in the possession of J.A. Schlosser). Whether any of the types are still in existence is unknown".

Type locality

Type locality fixed as Amboina by Andersen (1912: 707).

Specimens examined

INDONESIA

Ambon Island: Ambon, 3°41'S, 112°10'E, WAM M(38762, 38778, 38821–22, 38861, 42351, 42364) (4♀♀, 3♂♂).

Desa Amahusa, 3°41'S, 128°10'E, WAM M(43128, 43921) (1♀, 1 sex unknown)

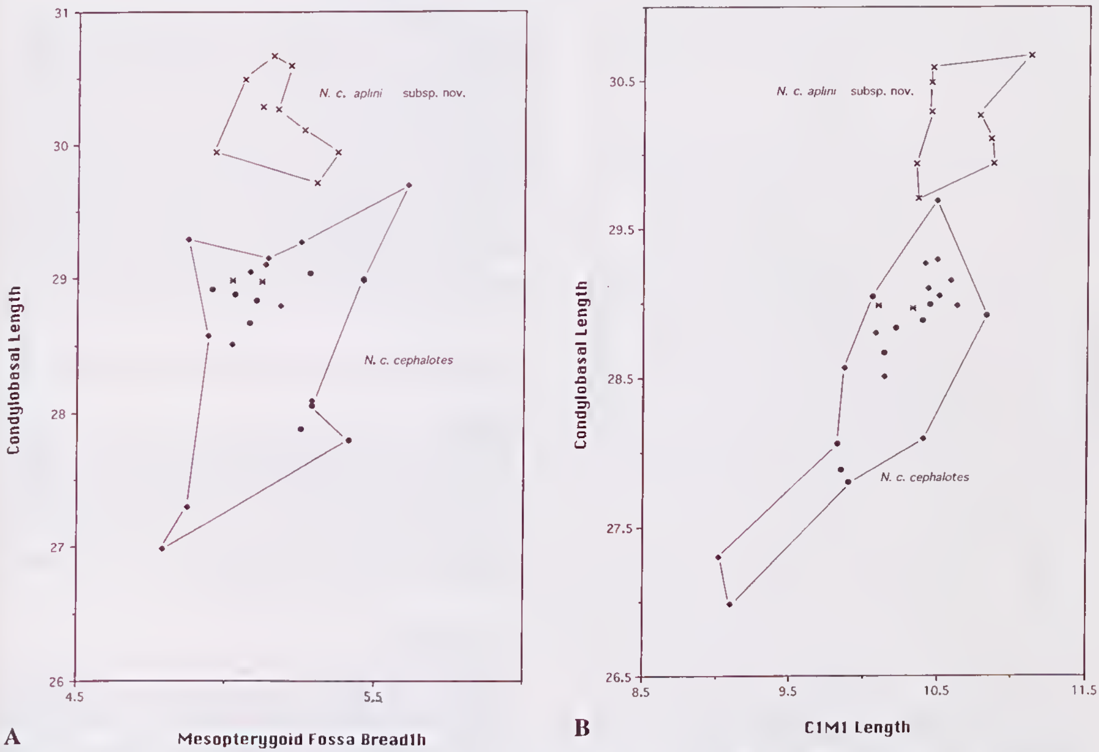


Figure 14 Plot of condylobasal length *versus* (A) mesopterygoid fossa breadth and (B) C^1M^1 length for individual *Nyctimene cephalotes*. Symbols as for Figure 2.

Buru Island: S.W. Buru, *c.* 3°40'S, 126°30'E, WAM M(43883–84) (2♀♀).

Seram Island:Kanikeh 3°06'S, 129°28'E, WAM M(34560–3, 34565) (1♀, 4♂♂). Solea, 2°53'S, 129°32'E, WAM M(34548, 34550–6, 34558–9 (3♀♀, 7♂♂).

Diagnosis

Nyctimene c. cephalotes differs from *N. c. aplini* as described in the earlier diagnosis of that subspecies.

Description

Skull moderately long 30.1 ± 0.68, narrow with braincase breadth 12.8 ± 0.37 and zygomatic width 19.8 ± 0.72; palate posterior margin V or sharp U shape; mesopterygoid fossa moderately wide 5.2 ± 0.20; C^1M^1 tooth row moderately long 10.2 ± 0.43; I^1 generally closely opposed to C^1, sometimes in contact with C^1; incisive foramen subcircular, small, generally not reaching posteriorly to a line joining P^2–P^2 anterior face; frontal between postorbital process flat or only very slightly basined.

Apart from the above characteristics and generally smaller size, the shape of the skull, dentary and dentition is very similar to *N. cephalotes aplini*.

Externals

Forearm moderately long 63.4 ± 2.07; ear moderately long 14.2 ± 0.61. Wing membrane generally connected between phalanx 1 of digits 2 and 3 (46%, N = 13) but also commonly from phalanx 1 of digit 3 (29%, N = 8) and commonly from phalanx 1 of digit 2 (25%, N = 7).

Pelage

Males and females with similar coloured dorsum but females with paler head, face and ventral pelage and paler patagia. The dorsal surface of males and females predominantly Drab but tipped with Olive Brown on shoulders and patchily with Fawn Color on lumbar and lower back regions; median dorsal stripe from crown of head to base of tail Olive Brown varying in breadth from 2–5. Hairs in mid dorsal region *c.* 11 long, basal one-third Drab. On head and behind ears to shoulders, Clay colour in males; in females a paler Straw Yellow. On face dark Smoke Gray in males; in females a paler Smoke Gray. Ventral surface in males Cream Color on chest and abdomen with neck and flanks Buff Yellow to Buff; in females

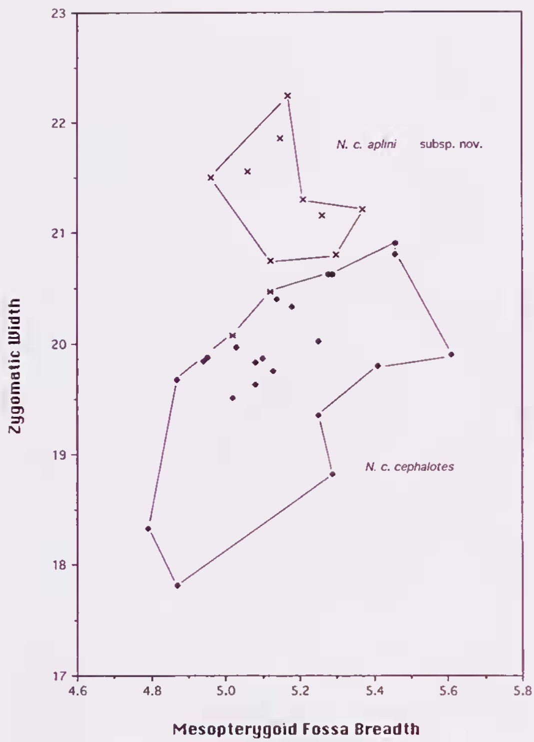


Figure 15 Plot of zygomatic width *versus* mesopterygoid fossa breadth for individual *Nyctimene cephalotes*. Symbols as for Figure 2.

ventral surface a uniform Cream Color. Patagia in males Olive Brown; in females a paler Fawn Color. Spots on patagia spectrum Yellow and distributed similarly to *N. cephalotes aplini*.

Distribution

Seram, Ambon and Buru Islands, Maluku Tenggara, Indonesia. It is unlikely that the *Nyctimene* from Timor Island attributed to *N. cephalotes* by Anderson (1912), Goodwin (1979) and Hill in Corbet and Hill (1992) is of that species. It is more likely to be associated with *N. keasti*.

Nyctimene keasti Kitchener, 1993

Nyctimene albiventer keasti Kitchener *et al.*, 1993: 408–412

Diagnosis

Nyctimene keasti differs from *N. cephalotes* as described in the earlier diagnosis of *N. cephalotes*. It differs from *N. albiventer* in averaging larger in all skull, mandible and external measurements. For example, greatest skull length 29.34 (28.04–30.78) 56 *v.* 26.98 (24.67–28.45) 45; braincase breadth 12.64 (11.64–13.94) 56 *v.* 11.93 (11.10–13.06) 45; zygomatic width 19.28 (18.11–20.40) 56 *v.* 18.07 (16.55–19.69) 45; C^1M^1 length 9.91 (8.39–10.50) 56 *v.* 8.82 (8.20–9.51) 45; forearm length 59.7 (55.1–63.0) 56 *v.* 54.9 (49.9–59.2) 48; and ear length 15.3 (14.2–16.9) 56 *v.* 13.2 (11.7–14.7) 48; forearm length generally longer relative to ear length (Figure 12); incisive foramen to posterior palate length, PIF, relatively greater relative to postorbital breadth (Figure 10); C_1M_2 length greater relative to M^1M^1 width (Figure 11).

Nyctimene keasti tozeri Kitchener, subsp. nov.

Holotype

Museum Zoologicum Bogoriense Number MZB 15904, adult male, weight 29.5 gm, carcase fixed in 10% formalin and preserved in 75% ethanol; skull and mandibles separate, liver preserved in ultrafreeze at WAM, collected by D.J. Kitchener and R.A. How on 27 April 1993.

Type locality

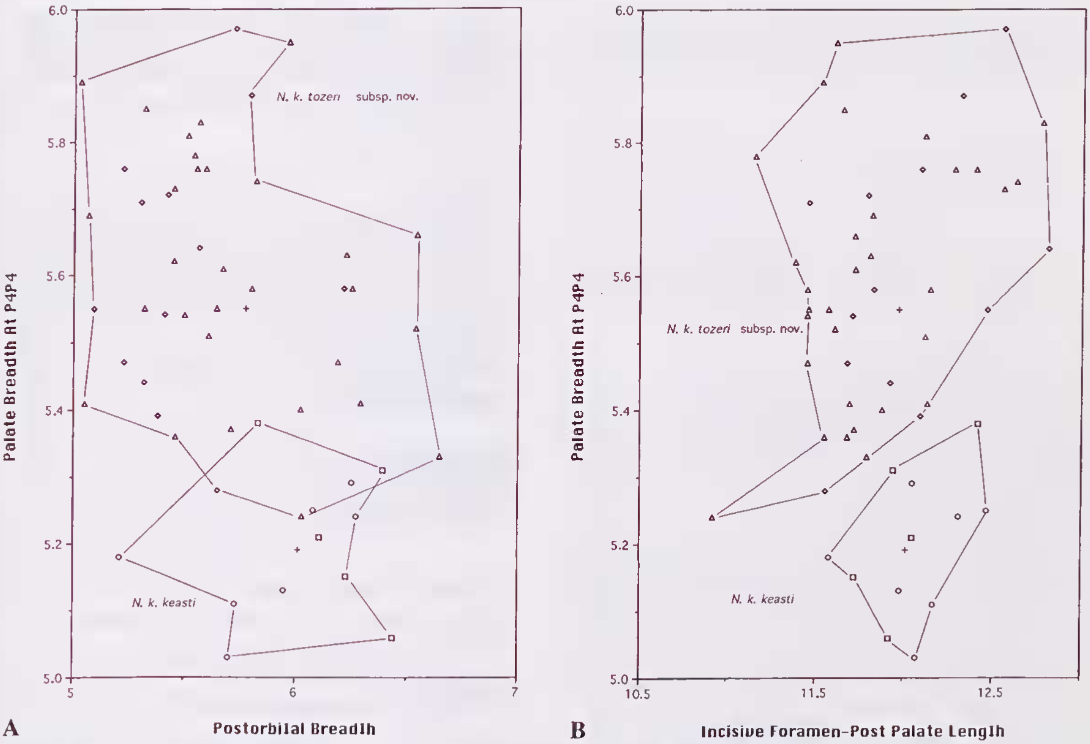
Lorulun (Figure 1) *c.* 20 km N Saumlaki, Yamdena Island, Tanimbar group; Maluku Tenggara, Indonesia (7°52'S, 131°25'E); altitude 200 m. Mist netted at *c.* 2m height in disturbed vine forest with the following genera of trees prominent: *Ficus, Erythrina, Podocarpus, Albizia* as well as 'Kenari' trees. The understory was mostly Lantana. There were numerous vines and creepers (see Kitchener and Maryanto 1994: Figure 5).

Paratypes

Yamdena Island: Desa Sifnana Omele, 7°56'S, 131°18'E, WAM 44398–401 (3♀♀, 1♂); Desa Lorulun (7°52'S, 131°25'E), WAM M(43776, 43782–88, 4394–95, 43798, 43801–06, 43809) (10♀♀, 8♂♂); Saumlaki, 7°59'S, 131°22'E, WAM M(43511–12, 43555–58, 43564–66, 43600) (8♀♀, 1♂). Selaru Island: Desa Adaut, 8°09'S, 131°08'E, WAM M(44201–05, M4408, M44300–03, M44310–11, M44316) (11♀♀, 2♂♂).

Diagnosis

Nyctimene keasti tozeri differs from *N. k. keasti* in averaging larger in all skull, mandible and external measurements, except for incisive foramen to posterior palate length (PIF) and postorbital breadth (Table 1). Palatal length between P^4P^4 lingual surface broader relative to both postorbital breadth and PIF (Figures 16 A,B, respectively); braincase breadth generally larger relative to postorbital breadth (Figure 17). It differs also from *N. k. keasti* in females having pelage of dorsum a similar dark Drab colour to that of males rather than females with a dorsum of Buff Yellow which is paler than the male Fawn color dorsum.



A B

Figure 16 Plot of palate breadth at P^4P^4 *versus* (A) postorbital breadth and (B) incisive foramen to posterior palate length for individual *Nyctimene keasti*. Symbols as for Figure 2.

Description

Skull, dentary and dentition

Intermediate sized skull with greatest length 29.5±0.56; zygomatic width 19.4±0.45; braincase breadth 12.7±0.29 and C^1M^1 length 10.0±0.34 (Table 1). Very similar in shape to *Nyctimene cephalotes aplini* except that the junction of the postorbital ridges and sagittal crest closer to postorbital process base and frontal area immediately anterior to this junction is less basined than is the case in *N. c. aplini*.

Externals

Forearm moderately long 60.1±1.12; ear moderately long 15.4±0.60. wing membrane usually attached to pes between phalanx 1 of digits 2 and 3 (56%, N=25); also commonly attached to phalanx 1 of digit 2 (16%, N=7), and phalanx 1 of digit 3 (27%, N=12) and rarely to between digits 3 and 4 at level of phalanx 1 (2%, N=1).

Pelage and patagia colouration very similar to *N. c. cephalotes*. Namely male and female dorsal surface of similar colour but with females having a paler head, face and ventral surface.

Distribution

Yamdena, Salaru and Larat islands, Tanimbar group, Maluku Tenggara, Indonesia.

Etymology

Named after Mr Tom Tozer, a distinguished retired gentleman, who for many years provided honorary assistance in the mammal section, Western Australian Museum, primarily with the curation of the Indonesian collection.

Referred specimens

The two specimens from Banda Neira Island, Band Group were included in the paratype series of *Nyctimene albiventer keasti* Kitchener, 1993 in Kitchener *et al.* (1993). These two specimens are treated as unallocated in the preceeding multivariate analysis because they are not readily attributable to either *N. cephalotes* or *N. keasti*. They may represent a distinct form of *Nyctimene* but if referrable to a recognisable form of *keasti*, they are clearly associated with *N. k. tozeri*. The taxonomic relationships of the Banda Island form will be clarified when more specimens become available for study.

The specimen WAM M34549, adult male, alcohol and skull specimen, collected from Solea, Seram, was included in all the preceeding statistical analysis as an unallocated specimen. It has a short forearm (58.0) and skull and external measurements similar to *N. keasti tozeri*. It was clearly allocated to this taxon in the DFA.

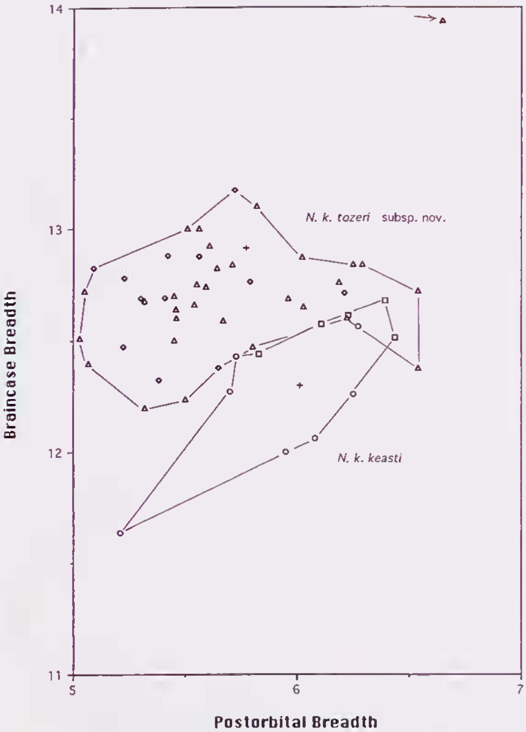


Figure 17 Plot of braincase breadth *versus* postorbital breadth for individual *Nyctimene keasti*. Symbols as for Figure 2.

Nyctimene albiventer albiventer (Gray, 1863)

Cynopterus albiventer Gray, 1863: 261–63

Holotype
The Natural History Museum, London Number BMNH 62.10.21.5; adult, 'cabinet' skin and skull, collected by Dr. A.R. Wallace in 1861.

Type locality
Morotai Island, Maluku Utara, Indonesia (*c.* 2°30'N, 128°30'E)

Specimens examined
Listed in Kitchener *et al.* (1993)

Diagnosis
Nyctimene albiventer albiventer differs from *N. a. papuanus* in averaging smaller in all measurements except rostrum length (see Kitchener *et al.* 1993: Table 1). Forearm length generally smaller relative to ear length (Kitchener *et al.* 1993: Fig 4) and palatal breadth at P^4P^4 generally smaller relative to rostrum length (Kitchener *et al.* 1993: Figure 3b).

If differs from *N. albiventer* subsp. indet. from Aru Island in averaging smaller in all measurements, except rostrum length, mesopterygoid fossa breadth and snout to vent length (see Kitchener *et al.* 1993: Table 1). P^4P^4 breadth also smaller relative to greatest skull length (see Kitchener *et al.* 1993: Figure 3a); and ear length longer relative to forearm length (see Kitchener *et al.* 1993: Figure 4).

Description
A small subspecies of *N. albiventer* with greatest skull length 25.68 ± 0.60 and forearm length 51.2 ± 1.2 (see Kitchener *et al.* 1993, Table 1). The overall shape of skull, dentary, and dentition similar to *N. cephalotes aplini*. Its pelage and colour are similar to that described earlier for *N. c. cephalotes*. Wing membrane attached to pes on phalanx 1 of digit 3 (Andersen 1912: 701).

Distribution
Morotai, Gilolo, Ternate and Goal area, N. Halmahera Island.

Nyctimene albiventer papuanus K. Andersen, 1910

Nyctimene papuanus K. Andersen, 1910: 621.

Holotype
The Natural History Museum, London Number

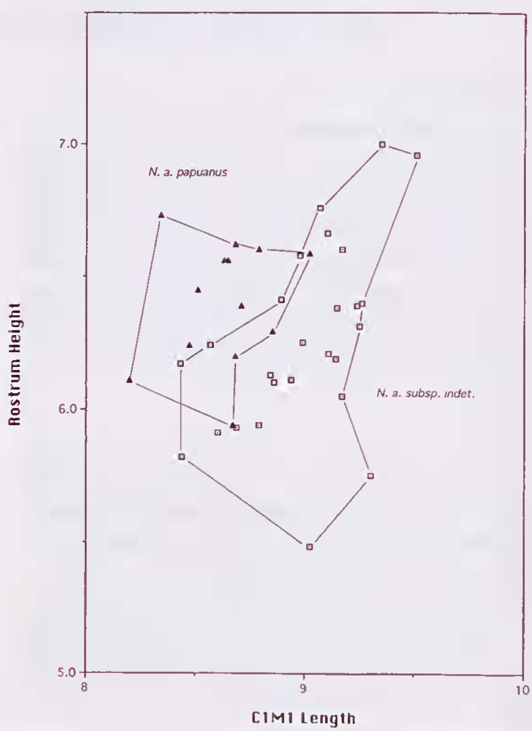


Figure 18 Plot of rostrum height *versus* C^1M^1 length for individual *Nyctimene albiventer* subsp. indet. and *N. a papuanus*. Symbols as for Figure 2.

BMNH 99.12.3.2, adult male, 'cabinet' skin, skull and mandibles separate, collected by A.S. Meek on 19 March 1899.

Type locality
Milne Bay, Papua New Guinea, (*ca.* 10°20'S, 150°30'E)

Species examined
Listed in Kitchener *et al.* (1993)

Diagnosis
Nyctimene albiventer papuanus differs from *N. a. albiventer* as described in the earlier diagnosis of that species.

It differs from *N. albiventer* subsp. indet. from Aru in having skull, tooth row and external measurements that generally average smaller. Rostrum height generally less relative to C^1M^1 length (Figure 18).

Description
Intermediate in overall skull, dentary, dental and external characters between *N. a. keasti* and *N. a. albiventer* (for measurements see Kitchener *et al.* 1993: Table 1).

Pelage colour similar to earlier *N. c. cephalotes* description. Wing membrane attached equally commonly to phalanx 1 of digit 2 (47%, N = 7) or at this level between digits 2 and 3 (53%, N = 8). Andersen (1912) stated that in the 14 specimens of *papuanus* he examined, this membrane was usually attached to phalanx 1 of digit 2 (79%, N = 11), and occasionally between digits 2 and 3 at level of phalanx 1 (14%, N=2) and on phalanx 1 of digit 3 (7%, N = 1).

Distribution
Irian Jaya: Andai, Skiu. Papua New Guinea: Eaga, Stephansort, S. Coast, Milne Bay; Olsbip, Upper Fly River; near Wewak, E. Sepik; near Baku, Gogol Valley, Madang; Lobota Cave, and Buso, Morobe. Admiralty Island and Bismark Archipelago (Andersen 1912, Hill 1983).

Nyctimene albiventer subsp. indet.

Diagnosis
This is a large form of *N. albiventer* which has the overall shape of the skull, dentary, dentition and colour of pelage of *N. a. papuanus* (for measurements see Kitchener *et al.* 1993: Table 1). It may be diagnosed against *N. a. albiventer* and *N. a. papuanus* as described in the earlier diagnoses of those subspecies.

The wing membrane attaches to the pes usually on phalanx 1 of digit 2 (62%, N = 10) but also commonly at level on phalanx between digits 2 and 3 (25%, N = 4), or on phalanx 1 of digit 3 (13%, N = 2).

Distribution
Wokam Island, but probably all other islands in the Aru group.

Specimens examined
Listed in Kitchener *et al.* (1993)

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